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Trophic interactions affecting a key ecosystem component: a multi-stage analysis of the recruitment of the Barents Sea capelin

Dag Ø. Hjermann[1*], Bjarte Bogstad[2], Gjert E. Dingsør[2], Harald Gjøsæter[2], Geir Ottersen[3], Anne Maria Eikeset[1], and Nils Chr. Stenseth[1,4]

[1] *Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, PO Box 1066 Blindern, N-0316 Oslo, Norway.*
Tl: +47.22.85.47.95, Fax: +47.22.85.40.01, Email: d.o.hjermann@bio.uio.no, n.c.stenseth@bio.uio.no
[2] *Institute of Marine Research, P.O. Box 1870 Nordnes, N-5817 Bergen, Norway*
[3] *Institute of Marine Research, Gaustadalléen 21, N-0349 Oslo, Norway*
[4] *Flødevigen Marine Research Station, Institute of Marine Research, NO-4817 His, Norway*
* *Contact author*

ABSTRACT

In the Barents Sea, capelin is a key food item for the North-East Arctic cod stock. This capelin stock has had very unstable population dynamics since 1985, with recruitment failures leading to three major collapses of the stock (>90% reduction of the stock size), resulting in decreased growth and survival of cod. Here we analyze in detail how predation and harvest affects the recruitment of capelin, using data on three different stages (i.e., larvae, zero-group and 1-year-olds) through the first 1.5 years of the capelin's life. We demonstrate that both herring predation (on capelin larvae) and cod predation (both on spawners and on offspring) has had major negative effects on capelin recruitment. Mortality is furthermore demonstrated to be strongly density-dependent, and is lower when temperatures are high – probably due to higher food availability for capelin. Harvesting maturing capelin on the way to the spawning grounds did affect the production of larvae, at least during the first half of the 1980s. However, the reduced production of larvae appears to a large extent to have been compensated by decreased density-dependent mortality on later life-stages, resulting in only minor effects on the abundance as 1-year-olds. Altogether, our study points to the importance of trophic interactions in determining the dynamic structure in high-latitude marine ecosystems.

Keywords: stock collapse, predation, trophic interactions, harvesting, density-dependent mortality, Generalized Additive Models (GAM)

Contact author: Dag Ø. Hjermann (d.o.hjermann@bio.uio.no), Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, Norway

Introduction

The capelin (*Mallotus villosus*) is a key species in several ecosystems in the North Atlantic (e.g., Carscadden et al. 2001). In the Barents Sea ecosystem, it forms a very large population (biomass up to 6 million tonnes), but the stock has collapsed to a small fraction of that three times since 1980 (Fig. 1). During these collapses, the entire ecosystem is changed (Gjøsæter et al. 2009). First, capelin is the only species able to effectively exploit the rich plankton bloom along the ice edge (Gjøsæter & Loeng 1987, Hassel et al. 1991, Gjøsæter et al. 2002). The herring does not go as far north as the capelin, and the plankton-feeding polar cod (Boreogadus saida) tolerates cold waters, but forages further down in the water column and not as effectively as the capelin (Hamre 1994). As a result, the autumn zooplankton biomass in the central/northern Barents Sea increases substantially during periods when the capelin stock is collapsed (Dalpadado and Skjoldal 1996, Dalpadado et al. 2001). Second, the capelin effectively transports a substantial amount of energy from the remote central and northern Barents Sea to the coastal areas, where it becomes easily available for piscivorous fish, seabirds, mammals and fishery restricted to the southern parts of the Barents Sea. In contrast, much of the biomass accumulated by the herring is moved out of the Barents Sea when the three-year old herring returns to the Norwegian Sea. Third, the availability of capelin is very important for several populations of piscivorous fish, mammals and birds (Dolgov 2002).

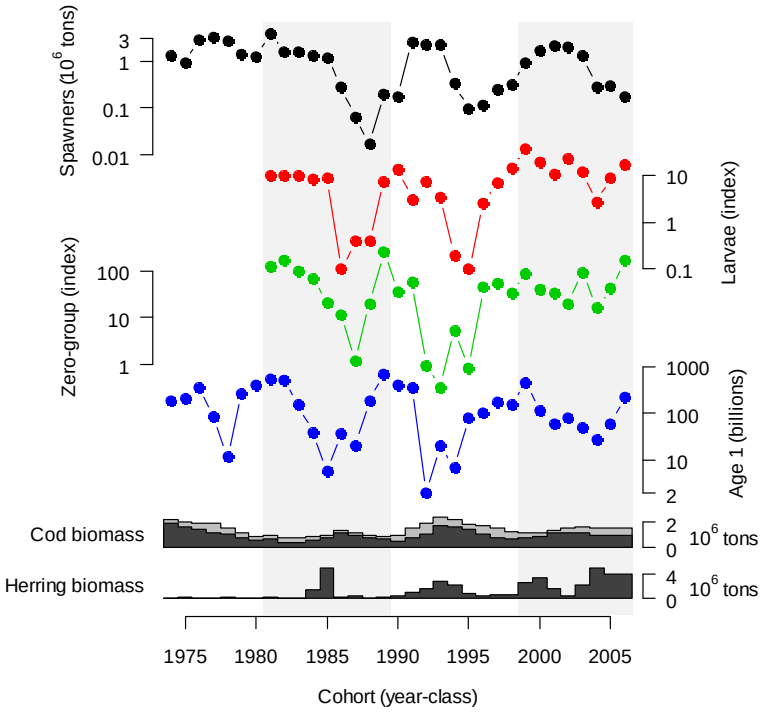

Fig. 1. Abundance of capelin cohorts 1974-2006 on stages 1-4. Note logarithmic y-axes. Spawners are represented by biomass of maturing fish (MSB_{t-1}). Age 1 data are for year t+1. The two bar plots on the bottom shows the biomass of the capelin predators cod (age 3-13: light grey, age 3-6: black) and young herring (for the bar plots, the x axis refer to year). The four periods used in the analysis are indicated by the vertical shaded areas.

Some populations, such as the Bear Island population of common guillemot (*Uria aalge*) appears to be specialized on capelin. In the case of cod, signals from several decades of data indicates that cod recruitment is depressed in periods with little capelin (Hjermann et al. 2007), and that capelin abundance has a strong effect on cod population growth (Durant et al. 2008). Finally, in years following a good reproduction of herring, the biomass of juvenile (1-2 yaer old) herring is able to block the reproduction of capelin, replacing a large capelin biomass with a small herring biomass (Hamre 1994, Gjøsæter and Bogstad 1998). Herring reproduction success is strongly and positively correlated with tenmperature, so high temperatures has a lagged negative effect on capalin (Hjermann 2004a) leading to large changes in the ecosystem at all levels, and a generally poorer transfer of energy from low to high trophic levels (von Quillfeldt et al. 2002).

The background of this paper is a paper published in 2004 by some of the authors of the present CM paper (Hjermann et al. 2004b). In this paper, existing knowledge ande hypotheses about capelin population dynamics were synthesized in a simple, close life-cycle model for capelin, which was fit to abundance estimates of capelin and its predators covering the years 1973–2001. This model was able to mimic the capelin collapses of the 1980s and the 1990s when using herring and cod abundance and harvest effort. There are three main motivations for the present analysis. (1) Hjermann et al. (2004b) only used data on age-specific abundance from age 1.5 years onwards, while there also exist data from two more stages during recruitment: the larvae and zero-group stage. These data are analysed in this study, enabling a much better understanding of capelin recruitment. (2) The capelin stock has collapsed a third time during the 2000s, and wanted to see if the dynamics of this collapse is in line with the collapses of the 1980s and 1990s. (3) Hjermann et al. (2004b) found that the model's ability to reproduce the collapse 1983–1986 profoundly reduced if harvesting was deleted from the model, a finding which they interpreted as "suggesting the importance of overexploitation during the first collapse". This conclusion did not agree with previous studies (e.g., Gjøsæter 1995) and led to a controversy about the role of harvesting during this collapse. In this CM paper, we show that the interpretation of Hjermann et al. (2004b) was wrong, and that harvesting probably played only a minor role in the collapses, including the first one in the 1980s.

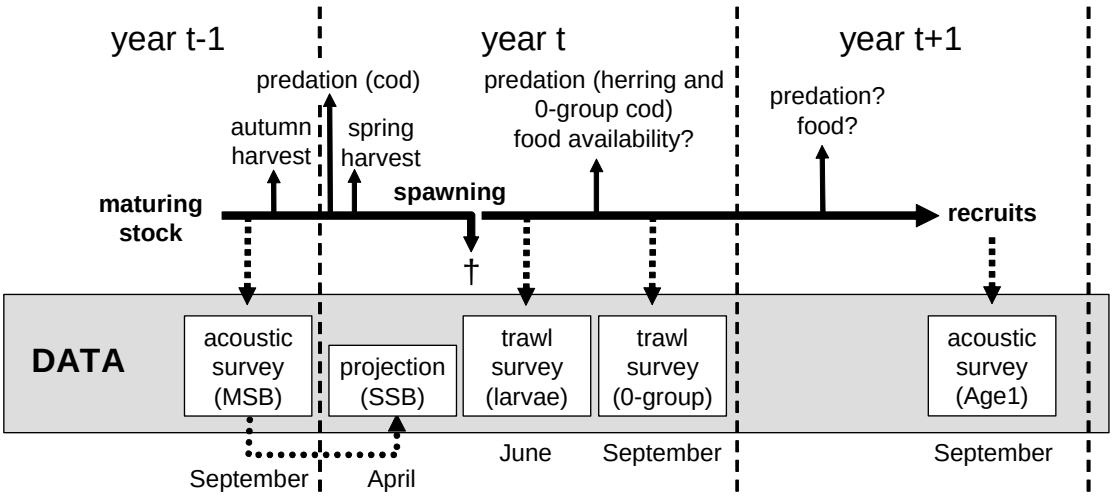

Fig. 2. An overview of capelin recruitment process and the capelin survey data used in this paper. Also see Tab. 1-3.

Methods

We used regression analyses to investigate how the transitions from stage to stage between spawners and age 1 (Tab. 1, Fig. 2) depended on biotic and abiotic covariates. In addition, we analysed the recruitment from stage 1 to stage 4 (i.e., the stock-recruitment relationship). We used Generalized Additive Models (GAM) models on the form

$\log(Stage_{i,j}) = a + G(\log(Stage_{i-1,j})) + H(X_j) + \ldots + \varepsilon_j$

where $Stage_{i,j}$ is the abundance at stage i (i = 2,3,4) in cohort j (j = 1981,1982, …,2006) and X is a covariate. The functions G and H may be linear (i.e., $b \cdot LogMSB_{t-1}$), or non-linear (e.g., a spline function); for further explanation, see e.g., Dingsør et al. (2007). There may be several covariate terms (X's); the covariates tested, based on capelin biology and prior knowledge (Fig. 2), are given in Tab. 3. Models (i.e., covariates) were selected on the basis of the General cross-validation (GCV) score.

The flip side of the versatility of GAMs non-linear functions is that it makes GAM even more prone to spurious correlations (Megrey et al. 2005). In our analysis, we tried to decrease this effect by only allowing monotonous effects. If the GAM analysis returned a non-monotonous relationship (i.e., shaped like "U" or "∩", e.g., a positive effect of cod at low cod abundance, and a negative effect of cod at high cod abundance), we considered it to be a likely to be a spurious result, explaining an unrealistically high fraction of deviance. In such cases, we replaced it with a monotonous relationship using "hockey stick GAM" (HSGAM), the GAM equivalent of hockey stick regression (e.g., Maceina 2007). That is, we restricted the relationship to be flat (slope zero) below or above some threshold (chosen by minimizing residual variance).

Tab. 1. Data of capelin abundance.

Stage	Cohorts	Month	Method	Reference
1. Spawners				
Maturing stock biomass (MSB)	1974-2006	Sept (0.5 yr before spawning)	Acoustic measurements; individuals larger than 14.0 cm are assumed to spawn	Gjøsæter et al. 1998
Spawning stock biomass (SSB)	1974-2006	April	Projected from MSB, accounting for losses due to fisheries and natural mortality[1]	
2. Larvae	1981-2006	June	Pelagic trawl data; incomplete coverage some years[2]	ICES 2006
3. 0-group	1981-2006	September	Stratified sample mean of pelagic trawl data from the international zero-group survey	Dingsør 2005, ICES 2007
4. Age 1	1974-2006	September	Acoustic measurements[3]	Gjøsæter et al. 1998

[1] The natural mortality rate used is based on the observed natural mortality between the surveys in year t-1 and t. The natural mortality of 1- and 2-year olds was assumed to be the same as the observed age 1-2 natural mortality, while the natural mortality of older fish was assumed to be the same as the observed age 2-3 natural mortality

[2] Due to restrictions on entering the Russian Exclusive Economic Zone (EEZ) in some years. Based on larvae distribution maps, the abundance might potentially have been significantly underestimated in the years 1996-1999, 2001-2002 and 2004. The possible effect of this bias was tested in transitions 1-2 and 2-3 using a dummy variable for the given years, and we found no effect in the expected direction.

[3] For the years prior to 1981, we use back-calculated values of survey abundance at age 2 the following year, since survey coverage of 1-year-old fish was poor during this period.

Tab. 2. Covariates used in the study. For sources, please contact the author.

Covariate	
$RelCatch_t$	Catch of maturing (>14 cm) capelin relative to MSB
$Herr12_t$	Biomass of young (age 1-2) herring
$CodSubad_t$	Biomass of cod age 3-6 (i.e., subadult piscivorous cod, expected to overlap with capelin in the winter months)
$CodAll_t$	Biomass of cod age 3-13 (i.e., all piscivorous cod)
$CodZero_t$ [1]	Abundance index of zero-group cod
$TempWintspr_t$	Average sea temperature at 0-200 m depth in the Kola section in winter/spring (December year *t-1* to June year *t)*
$TempSummer_t$	Average sea temperature (°C) at 0-200 m depth in the Kola section in summer (June-August year *t*)
$ZooSouth_t$ [2]	Average biomass of zooplankton in the six innermost stations of both transects of Nesterova (1990) (i.e., the North Cape transect and the Kola transect). Positions are 25º29'-23º12' E, 71º26'-72º27' N and 33º30'E, 69º30'-70º45' N for the two sets of stations.
$ZooNCSouth_t$ [2]	Average biomass of zooplankton in the six innermost stations of the North Cape transect (25º29'-23º12' E, 71º26'-72º27' N). In most years, this transect is most representative for capelin spawning grounds, as there is little spawning as far east as the Kola transect.

[1] Available for the period 1981-2006; only used for the stage 2-stage 3 transition
[2] Available for the period 1973-1990; only used for the stage 1-stage 4 transition

In order to investigate whether the results were time-dependent, we divided the total time series into four periods, and tested whether the model was improved by including the interaction between period and each of the variables of the model (i.e., a GAM version of ANCOVA). The periods were: 1974-1980 [=Period 1], 1981-1989 [=Period 2], 1990-1998 [=Period 3], 1999-2006 [=Period 4]). The first period was chosen on the basis of data availability: larval and zero-group data were not available for these cohorts, so the stage-wise analyses were not performed for period 1.

We checked the resulting model by plotting model residuals as well as testing for autocorrelation in the residuals (if all relevant variables have been taken into account we don't expect any autocorrelation). Also, the robustness of the models was tested using k-fold cross-validation (Fielding and Bell 1997): the time series (length N) is divided in k (more or less) equally long parts (k = 5 or 6 for time series starting in 1981 or 1974, respectively); then, the response variable ($\log(Stage_{i,j})$) was predicted for each part based on a regression excluding that part of the data.

Results and discussion

For all transitions, we found models that were able to explain over half of the variation (56-80% of the deviance explained, Tab. 4). Model residuals were not significantly autocorrelated at lag 1 and 2 years; overall, there were not more autocorrelations with $p<0.05$ than expected by chance. The k-fold cross-validation tests showed that the models were quite robust, i.e. returned quite good out-of data predictions in most cases, except for the stage 2 to 3 (larvae to zero-group) transition (commented further below).

Tab. 3. Potential explanatory variables tested for each transition. A minus or plus sign indicates the a priori expectation of the sign of the relationship (e.g., predators have negative effects). An empty cell indicates that the variable was not considered. We never considered two temperature or two cod variables in the same model.

	Transition between stages			
Covariate	**1-2**	**2-3**	**3-4**	**1-4**
$RelCatch_t$	-			-
$Herr12_t$		-	-	-
$CodSubad_t$	-		-	-
$CodAll_t$	-		-	-
$CodZero_t$		-	-	
$TempWintspr_t$	+/-		+/-	+/-
$TempSummer_t$		+/-	+/-	+/-
$ZooSouth_t$				+
$ZooNCSouth_t$				+

We will focus on three aspects of the results (Tab. 4, Fig. 3-6): (1) effects of predation, (2) effects of harvesting and density-dependence, and (3) effects of climate.

(1) Predation for cod and herring appears to be very important on all stages of capelin recruitment. In transition 1-2 (Fig. 3), the effect of cod is likely to indicate cod predation on spawners as they approach the spawning sites on the coast of Norway. In transition 2-3 (Fig. 4), from larvae to zero-group, it reflects predation by herring and 0-group cod on larval capelin as the capelin larvae drifty offshore from the spawning sites close to the coast. In transition 3-4 (Fig. 5), the analysis indicates that either cod or herring abundance affects survival in the one-year period following the zero-group stage (based on the size and spatial distribution of the capelin at this stage, that the model with cod has most credibility). Also, both herring and cod abundance affects the stock-recruitment relationship (Fig. 6).

(2) Harvesting clearly affects the abundance of larvae (Fig. 3; P = 0.04). However, harvesting did not affect abundance at recruitment at age 1 (Fig. 6). In fact, the abundance of spawners has practically no effect, statistically, on recruitment at the age 1-stage. The reason for this is that mortality is heavily density-dependent between the larval stage and age 1. This can be seen from the slope of $\log(Stage_{i-1,j})$, which is expected to be 1 if there is density-dependence. This slope is close to 1 (0.94) for the stage 1-2 transition, i.e. spawning/early larval stage (Tab. 4a), but 0.45 for the stage 2-3 transition (Tab. 4b) and <0.61 for the stage 3-4 transition (Tab. 4c). Thus, a reduced spawning stock, either due to fishing or natural causes (predation), leads to fewer larvae, but also to a compensatory reduction in mortality after the larval stage.

(3) Climate has a clear-cut effect on larvae (Fig. 3) as well as on the stock recruitment relationship (Fig. 6): warmer conditions is, everything else being equal, associated with better recruitment. Note that everything else tends not to be equal: there tends to be more predators (herring and cod) in warmer periods (Hjermann et al. 2004b). In this area, high sea temperatures are associated with higher primary production as well as higher influx of zooplankton from the Norwegian Sea (Dalpadado et al. 2003, Wassmann et al. 2006). However, we did not find that zooplankton biomass in spring and early summer affected recruitment positively. The reason may be that zooplankton biomass for a large part is determined by the abundance of *Calanus finmarchicus*. In contrast to herring and cod, capelin larvae mainly eat a variety of zooplankton and to not be closely coupled to *C. finmarchicus*, (Fossheim 2006). Instead, the relationship between temperature and capelin

Tab. 4. The optimal models found using model selection. Only models using MSB (maturing stock biomass) are shown; results using SSB (spawning stock biomass are referred to in the text. Coefficient estimates are given in the cases when the effect was found to be linear of hockey-stick-shaped. The importance of each term is indicated by ΔDev, the decrease in proportion of deviance explained when the term is deleted from the model (when the term was involved in an interaction term, this term was deleted too).

(a) Stage 1 to stage 2 (larvae), using MSB for stage 1 (74% of the deviance explained)						
	edf	**Estimate**	**SE**	**F**	***p***	**ΔDev.**
Intercept	1	-3.70	1.53	5.85	0.025	
$\log(MSB_{t-1})$	1	0.94	0.18	27.95	<0.001	0.34
$CodSubad_t$	1	-3.14	0.59	28.02	<0.001	0.34
$RelCatch_{t-1}$	1	-2.94	0.91	10.54	0.004	0.13
$TempWintspr_t$	1	0.80	0.39	4.29	0.051	0.05
(b) Stage 2 (larvae) to stage 3 (zero-group) (64% of the deviance explained)						
	edf	**Estimate**	**SE**	**F**	***p***	
$\log(Larvae_t)$	1	0.45	0.15	9.09	0.007	0.13
$\log(Herr12_t)$	1.66			1.54	0.238	0.22
$CodZero_t$	1	-0.039	0.013	9.33	0.006	0.22
$\log(Herr12_t)*CodZero_t$	1	-0.049	0.016	9.47	0.006	0.17
(c) Stage 3 (zero-group) to stage 4 (one-year olds)						
	edf	**Estimate**	**SE**	**F**	***p***	
Model 1 (75% of dev. expl.)						
$\log(Zero_t)$	1.52			6.86	0.005	0.12
$\log(Herr12_t)$ (when < -0.24)		0				
$\log(Herr12_t)$ (when ≥ -0.24)	1	-1.41	0.31	20.60	0.000	0.21
$TempWintspr_{t+1}$ (when < 3.79)		0				
$TempWintspr_{t+1}$ (when ≥ 3.79)	1.09			5.05	0.016	0.09
Model 2 (66% of dev. expl.)						
Intercept	1	5.19	1.01	26.40	0.000	
$\log(Zero_t)$ (when < 1.81)		0				
$\log(Zero_t)$ (when ≥ 1.81)	1	0.61	0.22	7.94	0.010	0.12
$CodSubad_{t+1}$	1	-1.92	0.74	6.69	0.017	0.10
(d) Overall recruitment (stage 1 to 4), using MSB for stage 1 (56% of the deviance explained)						
	edf	**Estimate**	**SE**	**F**	***p***	
$\log(MSB_{t-1})$	1	0.16	0.15	1.06	0.312	0.03
$\mathrm{Log}(Herr12_t)$	1.79			10.59	0.000	0.35
$CodAll_{t+1}$	1.62			3.99	0.030	0.13
$TempWintspr_{t+1}$	1	1.63	0.40	16.45	0.000	0.29

recruitment may be linked to oceanographic features such as eddies and coastal jets. Fossheim et al. (2006) suggested that an important factor for capelin recruitment can be the number and timing of short-lived springtime eddies, which carry warm, oceanic and plankton-rich water on to the shelf. However, compared to the beach-spawning capelin populations in Canada (Leggett and Deblois 1994), the effects of climate on the recruitment of this capelin stock seem to be relatively small.

The results above refer to using maturing stock biomass (MSB). We also did similar analysis for transitions 1-2 and 1-4 replacing MSB with SSB, which is intended to take

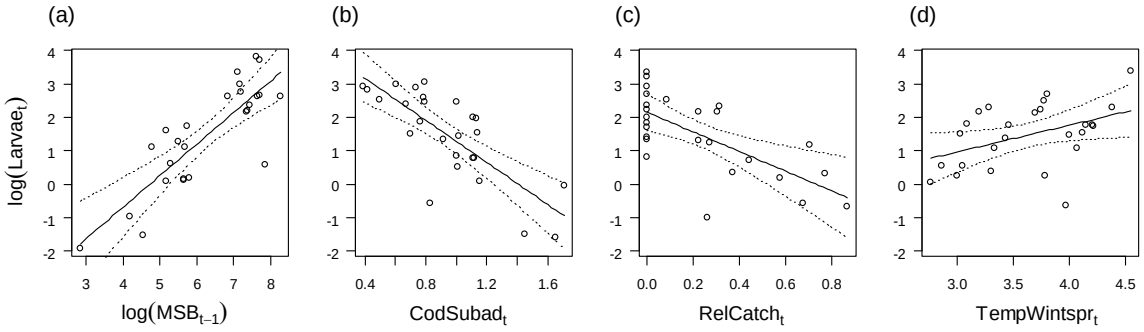

Fig. 3. Effects of abundance and covariates on the stage 1-2 transition.

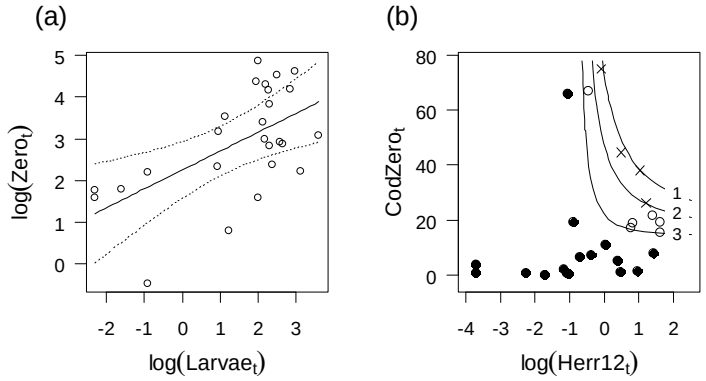

Fig. 4. Effects of abundance and covariates on the stage 2-3 transition. In (b), The contour lines indicate the predicted abundance of zero-group capelin (log(Zero$_t$)) adjusting for variation in log(Larvae$_t$), assuming log(Larvae$_t$) to be equal to the mean value. The symbols show the observed values of log(Zerot), adjusted for variation in larval abundance: log(Zero$_t$) <2 (crosses), log(Zero$_t$) between 2 and 3 (open circles), and log(Zero$_t$) >3 (closed circles).

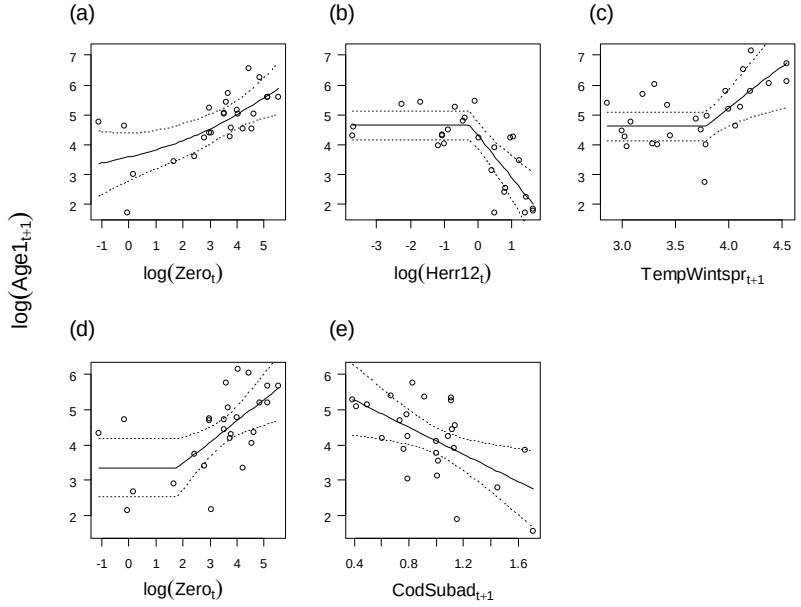

Fig. 5. Effects of abundance and covariates on the stage 3-4 transition. Top row (a-c) is model 1 referred to in Tab. 3, bottom row (d-e) is Model 2.

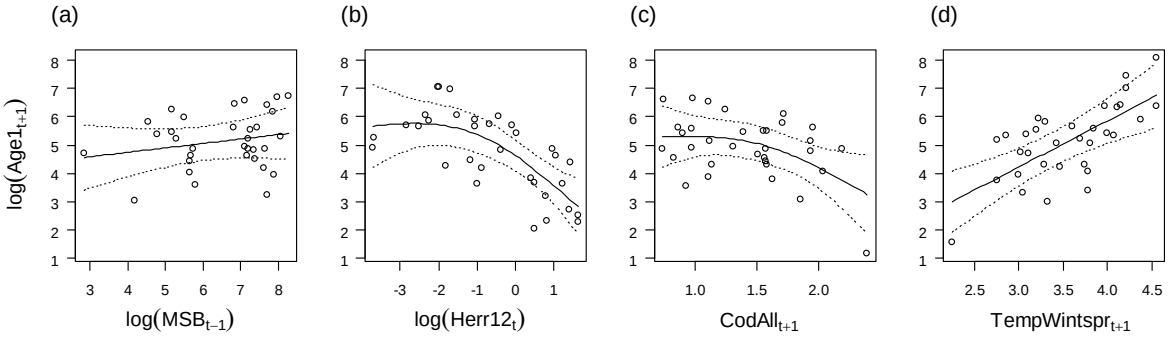

Fig. 6. Effects of abundance and covariates on the stage 1-4 transition, i.e., the stock-recruitment relationship.

into account capelin harvesting as well as interannual variation in natural mortality. In both these transitions, the harvesting effect disappeared when we used SSB, but cod abundance was still quite significant. This suggests that the way SSB is calculated (see Tab. 1) is able to effectively take harvesting into account, but not the variations in natural mortality of spawners due to cod predation.

All in all, the results confirm that capelin is strongly affected by predation on its young stages, a conclusion that now also is supported by field studies (Hallfredsson 2006, Hallfredsson and Pedersen 2007). Predation and harvesting on maturing/spawning capelin appears to have a smaller effects due to strong density-dependence between the larval stage and age 1.

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